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Dynamics of Nutrient Cycling in Plantation Ecosystems

H. G. MILLER

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I. INTRODUCTION

To ensure that soil nutrients are being efficiently exploited and that fertilizers are used to their greatest effect, the forest manager requires an understanding of the role of nutrient cycles in maintaining forest productivity. Mechanisms evolved by trees to enable growth despite limited soil nutrient supply include means of increasing input to the site, of maximizing retention within the ecosystem and of ensuring conservation and reuse of elements once they are in the tree. The relative importance of these different mechanisms varies between elements and alters as the stand develops. Clearly the cycle of potassium is very different between the young and old stands illustrated in Fig. 1, and at both stages rather different patterns would be shown by an element such as nitrogen that is less mobile within the tree and humus.

NUTRITION OF PLANTATION FORESTS
ISBN 0-12-120980-6

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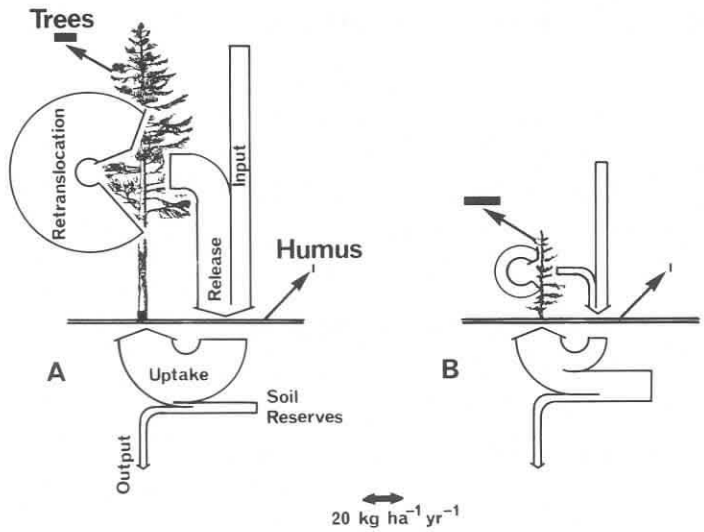

Fig. 1. Three levels of cycling are present in a plantation: one that leads to the input and loss of a nutrient, a second through the tree-soil system and the third represented by retranslocation within the tree. Illustrated are the patterns of cycling of potassium calculated (A) for 40-year-old and 11 m-tall *Pinus nigra* var. *maritima* and (B) for 10-year-old and circa 2 m-tall *P. nigra* var. *maritima*. Width of arrows are proportional to the fluxes they represent, and the lengths of the solid bars are proportional to the rates of accumulation in trees and humus, all to the common scale shown beneath the diagrams (data from Miller *et al.* in press).

Similarly the significance of these mechanisms may vary with species, in particular between evergreen and deciduous species, although information on the latter is scarce.

Indeed, the study of forest nutrient cycles in general, although arguably derived from the pioneering work of Ebermayer (1882) in the last century, is, in its modern form, barely 30 years old, so this chapter, in order to be comprehensive, will inevitably resort to speculation, but speculation based on a rapidly growing data base.

II. CYCLES WITHIN THE PLANTATION ECOSYSTEM

Nutrient ions taken up by a tree may be translocated into and out of a variety of tissues, where they may become involved in a range of growth processes or stored, before being either immobilized in accumulating structural tissues or released through litter fall, root death or crown leaching. As tissues senesce,

as at leaf abscission or during heartwood formation, nutrient ions, other than those irretrievably bound in structural tissues, are liable to be withdrawn back into the living tissues. Eventually any ion that it is impossible, or unnecessary, to conserve is released to accumulate in the soil organic layers. In northern latitudes, in particular, the litter and humus layers, where most feeding roots may be located, can contain a considerable reserve of many nutrients.

A. Accumulation and Release by Tree Stands

(1) Pattern of accumulation by tree stands

Nutrient concentrations vary greatly between component parts of trees and so the pattern of nutrient accumulation is very different from that of biomass. Furthermore, the nutrient-rich foliage and lateral roots reach their maximum development rather early in the rotation, whereas the biomass of woody, and hence nutrient-poor, structural organs accumulates progressively (Fig. 2). As a result, the rate of accumulation of most nutrients, excepting those such as Ca which are primarily located in structural tissues, is more rapid prior to and during canopy closure than at later stages. Indeed, reported variations in the distribution of nutrients between forest stands may simply reflect different development stages at time of sampling.

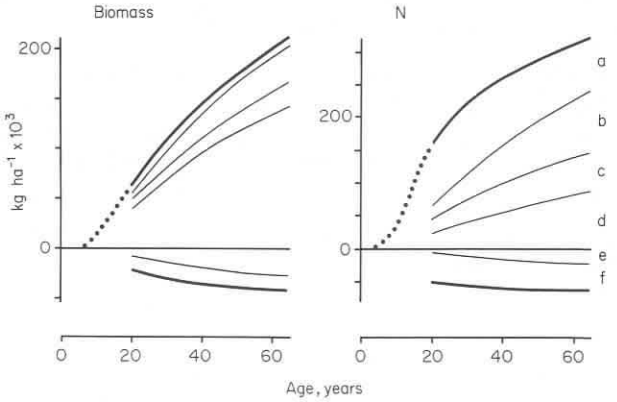

Fig. 2. Patterns of accumulation (kg ha^{-1}) of biomass and nitrogen in (a) foliage, (b) branches, (c) stem bark, (d) stem wood, (e) stump and (f) lateral roots for a managed plantation of *Pinus nigra* var. *maritima*. Data for ages 20 to end of economic rotation from Miller *et al.* (1980a, b), extrapolated back to time of planting by analogy with the pattern published by Madgwick *et al.* (1977). Stand height is 10 m at age 24 and 20 m at age 51 years.

For any given development stage, rate of accumulation is proportional to growth rate, which is broadly a function of latitude and species. There is also a possibility of differences between species and genera in nutrient concentrations, but a search of the literature reveals little support for consistent differences. Thus, in the values shown in Fig. 3 the only distinct difference is

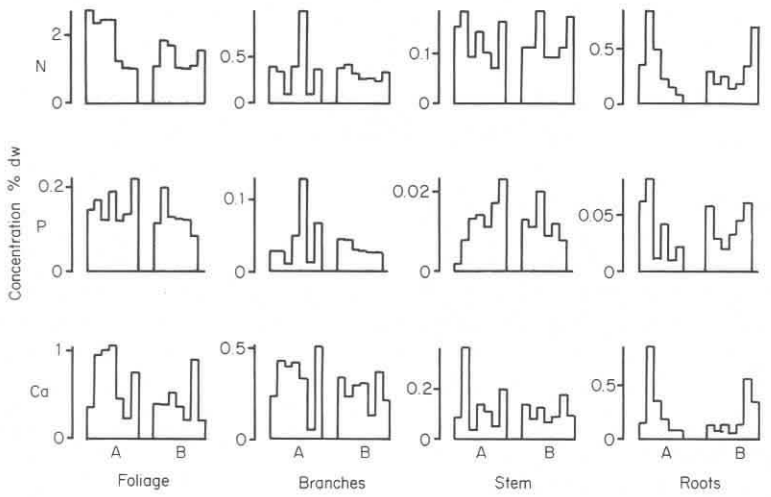

Fig. 3. Weighted mean concentrations (percent of dry weight) of nitrogen, phosphorus and calcium in foliage, branches, stems and roots for comparison (A) between four hardwood (first four bars) and three coniferous genera and (B) within the genus *Pinus*. Plotted values, from left to right, are (A) for (1) *Fagus sylvatica* (Sweden), (2) mixed *Quercus* spp. (Belgium), (3) *Alnus rubra* (Washington, USA), (4) *Betula pubescens* (Finland), (5) *Picea abies* (Germany), (6) *Tsuga heterophylla* (Oregon, USA), (7) *Pseudotsuga menziesii* (Washington, USA, no root values), and (B) for (8 and 9) two stands of *Pinus sylvestris* (Finland), (10) *P. patula* (Tanzania), (11) *P. nigra* (Scotland), (12) *P. taeda* (North Carolina, USA), (13) *P. echinata* (Tennessee, USA) and (14) *P. strobus* (North Carolina, USA, no P values). Stands 2 and 13 are on calcareous soils, whereas the rest are on acidic soils.

Sources: 1, 2, 3, 6, 7, 13 and 14, summary by Cole and Rapp (1981) of work by, respectively, Ulrich and Ellenberg, Duvigneaud *et al.*; Turner, Grier, Turner and Cole, Harris, Swank. 4, Mälkönen (1977); 5, Nihlgård (1972); 8 and 9, Mälkönen (1974); 10, Lundgren (1978); 11, Miller *et al.* (1980b); 12, Wells and Jorgensen (1975).

between the N concentrations in foliage of hardwood species and coniferous species. However, as *Larix* usually shows foliar N concentrations of around 2% (Everard, 1973), the difference is perhaps between deciduous and evergreen species rather than between groups of plant families. Otherwise, the results in Fig. 3 suggest little assortment by plant orders, group or families, variation within the *Pinus*, or even between the two stands of *Pinus sylvestris* (Scots pine), being often as great as that found between genera,

irrespective of family or group. Much of the same point was made by Tsutsumi (1971) who observed that the accumulated weight of nutrients in individual trees of nine different species, including coniferous and broad-leaved trees, showed a common linear relationship with dry weight of tree.

Comparison of trees between sites, however, may reveal appreciable differences in nutrient concentrations, even within species, and it would seem that generally soil supply has a greater influence than genetic factors on the concentration of nutrients in tree tissues. For example the two stands on calcareous soils in Fig. 3 show high Ca levels in all organs. Nevertheless, the extensive literature on critical nutrient concentrations in tree foliage (e.g. van den Driesshe, 1974; Binns *et al.*, 1980) suggests the possibility of some limited specific variation, particularly in levels of P. Apparent specific variations in the concentrations in other component parts of the tree are probably primarily the result of variations in morphology, rather than in any more fundamental aspect of the plant. Thus high mean concentrations of some elements in branches of *Picea abies* (Norway spruce) in Fig. 3, reflect the great number of small branches formed by this species, with consequent high ratio of nutrient-rich bark and phloem to nutrient-poor wood. As this ratio, and the ratio of nutrient-poor heartwood to the richer sapwood, alters with tree size, there will be a progressive shift in mean nutrient concentrations in branches and stem as the stand develops.

Rate of nutrient accumulation by a plantation, therefore, is a function of the rate of growth, the development stage, the availability of soil nutrients and, perhaps least significant of all, specific differences in optimum nutrient concentrations. However, species differences are important in so far as growth rates and size at maturity are under genetic control.

(2) Rate of release

(a) Release in litterfall. In managed forests, where mortality is prevented by regular thinning, foliage accounts for between 75 and 95% of the total litterfall, the remainder being branches, bark flakes and reproductive organs (Table I). If old or moribund forests are excluded, there is generally a close correlation between weight of leaf-fall and growth rate in managed forests, irrespective of species (Fig. 4), with the reported variations within a species often being similar to that between species (values for *Pinus sylvestris* range from 0.5 to 6.6 t ha^{-1} yr^{-1}). Bray and Gorham (1964) suggested that on average there is surprisingly little difference in rate of litterfall between evergreen and deciduous trees. Recent data from the International Biological Programme, on the other hand, gave values of 2.7 and 4.5 t leaf- litter ha^{-1} yr^{-1} for evergreen and deciduous forests, respectively (O'Neill and DeAngelis, 1981), although this may reflect a difference in average latitude

Table I. Weight and amounts of nutrients in different components of litterfall collected beneath *Pinus nigra* var. *maritima* aged 40 years and height 11 m.[a]

Plant part	Dry weight kg ha^{-1} yr^{-1}	Nutrient content kg ha^{-1} yr^{-1}		
		N	P	K
Foliage	3290	23.3	2.40	7.0
Twigs	235	0.8	0.07	0.1
Cones	13	0.04	0.004	0.006
Remainder[b]	132	1.0	0.07	0.1

[a] From Miller *et al.* (1970).
[b] Remainder comprised flowers, bud scales and bark flakes.

for the two groups. In the few areas where a direct comparison is possible, rates of litterfall are remarkabley similar (Table II).

It is reasonable to postulate that rate of leaf-fall throughout the rotation is broadly proportional to the rate of production of new foliage. As such, leaf-fall can be expected to increase very rapidly during canopy closure and thereafter parallel stem volume increment (Miller *et al.*, 1980b), at least until the age of maximum mean annual increment. At an advanced age, however, foliage and litter production continues, albeit at a reducing rate, even once

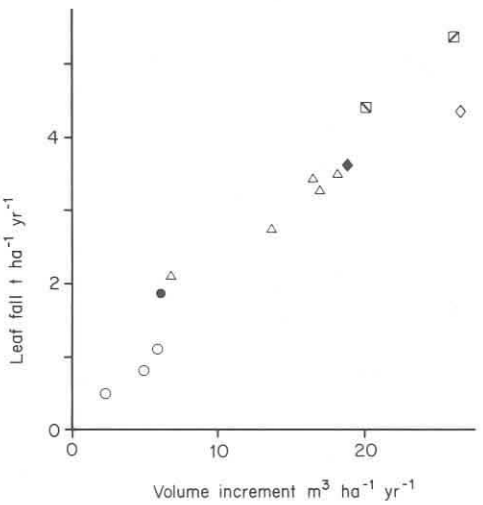

Fig. 4. Relationship between leaf-fall and volume growth in plantations and managed even-aged forests reported for three stands of *Pinus sylvestris* (○) in Finland (Mälkönen, 1974), *Betula pubescens* (●) in Finland (Mälkönen, 1977), *Picea abies* (◇) and *Fagus sylvatica* (◆) in Sweden (Nihlgård, 1972), *Pinus patula* (▨) and *Cupressus lusitanica* (▧) in Tanzania (Lundgren, 1978) and results from a N fertilizer trial (△) on *Pinus nigra* var. *maritima* (Miller *et al.*, 1976) in Scotland.

Table II. Comparison between species and sites in the amount and nutrient content of total litterfall.

Location	Latitude	Species	Age	Dry weight	Litter nutrient content		
				$t\,ha^{-1}\,yr^{-1}$	N%	P%	K%
Tanzania, Lushoto[a]	5°S	*Pinus patula*	20	6.2	0.66	0.03	0.14
		Cupressus lusitanica	20	5.2	0.71	0.04	0.10
Germany, Solling[b]	52°N	*Picea abies*	59	3.4	1.39	0.12	0.37
		Fagus sylvatica	80	4.0	1.34	0.11	0.43
Sweden, Kongalund[c]	56°N	*Picea abies*	55	5.6	1.04	0.09	0.19
		Fagus sylvatica	78	5.7	1.21	0.09	0.25
Sweden, Öved[d]	56°N	*Fagus sylvatica*	90	4.4	0.91	0.05	0.35
Långaröd		*Fagus sylvatica*	100	3.8	0.82	0.07	0.30

[a] Lundgren (1978)

[b] Ulrich and Ellenberg, reported in Cole and Rapp (1981)

[c] Nihlgård (1972)

[d] Nihlgård and Lindgren (1977), the soil at Öved was a rich mull gley soil as against an acid brown forest soil at Kongalund and a typical podsol at Långaröd.

net increment in stem wood virtually ceases. At this stage leaf-fall represents a large portion of both the net primary production and of the nutrient uptake (Attiwill, 1979).

As foliage ages many nutrients are translocated back into living tissues, a process that accelerates during the weeks just prior to abscission. From 60 to 85% of the major nutrients can be conserved in this way (Table III), an

Table III. Comparison of concentrations and amounts of nutrients in young foliage, in the oldest cohort of needles held on the tree (3-year-old) and newly fallen needle litter collected in a stand old 11 m tall *Pinus nigra* var. *maritima*.[a]

Plant part	Nutrient				
	N	P	K	Ca	Mg
	% Dry Weight				
First year needles	1.54	0.15	0.73	0.23	0.11
Old needles	1.25	0.12	0.63	0.45	0.10
Needle-litter	0.76	0.07	0.17	0.49	0.08
	mg per 100 needles				
First year needles	67	6	31	10	5
Old needles	53	5	26	18	4
Needle-litter	22	2	5	14	2
Proportion of nutrients retranslocated between year one and abscission	0.67	0.67	0.84	–	0.60

[a] From Miller *et al.* (in press).

exception being Ca, which accumulates with age and so is present in high concentrations in litterfall. Similar accumulations in litter have been noted for Cr, Fe, Zn, Cu and, in particular, Pb (Nilsson, 1972; Heinrichs and Mayer, 1980). Generally recovery through retranslocation from dying foliage is most efficient in trees receiving optimum rates of nutrient supply. At supra-optimum rates there is less need for recovery, whereas under deficiency conditions a greater proportion of the nutrient within a needle is incorporated in structural tissues and cannot be mobilized. Therefore, the "labile" pool may be much less than needle analysis of total nutrient would suggest.

Non-leafy components are responsible for a fairly small proportion of the nutrients released by trees, but can be higher than suggested in Table II if there is heavy flowering and fruiting. Thus, Rapp *et al.* (1979) measured 9.8 kg N ha^{-1} in the yearly fall of flowers, fruit and branches, compared with 26.4 kg in needles, beneath *Pinus pinea*.

Nutrient concentrations on leaf-litter, although reduced by retranslocation, are still functions of those in the fresh foliage (e.g. Miller *et al.*, 1976; Albrektson *et al.*, 1977). As neither foliar nutrient concentrations nor rate of

litterfall are strongly determined by species, the rate of release of nutrients in litterfall, like the rate of accumulation in tress, is primarily determined by growth rate and soil nutrient supply.

(b) Release through crown leaching. This is the loss into an aqueous solution bathing a plant surface of elements previously taken up by the plant. Invariably the cations K, Ca, Mg and Mn are easiest leached, although anions are also removed, and losses are greatest if a nutrient ion is present in excess of requirements (Tukey, 1970). Hydrogen ion exchange on the leaf surface can certainly account for much of the cation loss, but as anions are also leached there are clearly other processes involved.

It has long been known that rainwater beneath trees is enriched in many plant nutrients and Tamm (1953), in an important study, considered "salts leached out from the trees" to be a major source of nutrients for the moss *Hylocomium splendens* growing in the shade of *Picea abies*. However, not all the salts gained by rainwater passing through trees are the result of crown leaching, for rainwater also washes from the canopy elements derived from the atmosphere as aerosols, dust, gas etc. trapped on the surfaces of leaves and branches. Thus, data from a study in *Picea sitchensis* (Sitka spruce) (Table IV) suggests that the atmosphere could be a major source of Ca and

Table IV. Weighted mean concentrations of nutrients in rainwater collected over five years outside and within a stand of *Picea sitchensis* in Scotland.[a]

Component	Nutrient concentration (mgl^{-1})				
	N	P	K	Ca	Mg
Precipitation outside the stand	0.7	0.01	0.4	0.8	0.4
Throughfall and stemflow beneath the trees[b]	1.0	0.04	1.9	2.0	0.7
Precipitation beneath inert mesh[b]	0.8	0.01	0.5	1.6	1.4

[a] H. G. Miller and J. D. Miller (unpublished).

[b] The values for within the stand were corrected for increases resulting from evaporation of water intercepted by the trees. Concentrations in water collected outside the stand in gauges surmounted by vertical cylinders of polyethlylene coated wire mesh are also given.

Mg in water collected beneath trees whereas crown leaching is contributing large amounts of K.

Apportioning the measured gain of an ion in throughfall and stemflow into the separate contribution from crown leaching (which is part of the cycle internal to the ecosystem) and the contribution from elements trapped from the atmosphere (which represents an input to the ecosystem) presents particular problems of methodology. Recently, however, teams working with

Ulrich in Germany, Miller in Scotland and Lindberg in Tennessee have developed three very different techniques which, although none is ideal, appear to be producing reasonably similar results. Of the major elements, K is clearly leached to the greatest extent, amounts sometimes being comparable to those in litterfall (Table V). Similarly, results of Lindberg *et al.* (1979)

Table V. Comparison of annual flux of major nutrients in litterfall and crown leaching.

Species	Flux component	Flux ($kg\,ha^{-1}\,yr^{-1}$) N	P	K	Ca	Mg
Pinus nigra var. *maritima*[a]	litterfall	34.7	2.9	7.7	18.1	3.2
	crown leaching	−0.4	trace	6.0	1.5	3.0
Fagus sylvatica[b]	litterfall	49.0	4.0	16.0	16.2	1.6
	crown leaching	trace	−0.2	7.6	2.5	0.2

[a] Miller *et al.* (1976).
[b] Ulrich *et al.* (1976).

suggest that the release of Mn, Zn and Cd is primarily through crown leaching. With some elements, however, foliar uptake may dominate, giving negative leaching rates. For the *Pinus nigra* var. *maritima* (Corsican pine) in Table V it was found that net foliar leaching and net foliar uptake of N alternated throughout the year, leaching being dominant just prior to growth, again during the autumn litterfall and finally in mid-winter, all times of known high concentration of soluble amino acids in tree tissues. The annual rate of leaching of N was also found to vary with N fertilizer treatment.

Crown leaching, therefore, is a significant process but its importance varies between nutrients. Rate of leaching is also influenced by the quality of incident rainfall, in particular with acidity. Horntvedt *et al.* (1980) observed a doubling in the rate of leaching of calcium and magnesium from *Picea abies* crowns as the pH of artificially applied rain was lowered from 6.0 to 4.0. This, however, was not apparently accompanied by any change in growth rate nor in the nutritional health of the tree, which would not be the case if the rate of release in litterfall was to be doubled. Presumably elements released in crown leaching are readily reabsorbed by the roots and mycorrhizal hyphae, but information is lacking. Information is also insufficient to reach any clear conclusion as to possible species variations. Early work by Madgwick and Ovington (1959) indicated that these may occur, and recent work on *Picea sitchensis* (Table IV) suggests appreciable crown leaching of both N and P in this species, whereas, in contrast, very little movement of these elements was found in the studies on *Pinus nigra* and *Fagus sylvatica* (European beech) reported in Table V. Plants from mixed forests subjected to heavy and frequent rains may be adapted to resist leaching (Tukey, 1970).

(c) Release from Root Systems. There is a great dearth of information about the rate of root turnover. It seems that the pattern of biomass accumulation is rather as depicted in Fig. 2, there being a continued increase of stump and major structural roots, analogous to stem wood accumulation above ground, and a rapid build-up followed by a stabilized level, or even slow decline, of fine roots. These fine roots probably comprise very ephemeral feeding roots, perhaps less than 2 mm in diameter and with a life-span of often less than one year, carried on larger lateral roots that are most likely to be within the 3 to 8 mm diameter range and have a life-span of several years. Whereas foliage is produced and shed on a fairly strict schedule, growth and death of feeding roots seems to be essentially opportunistic, varying broadly with soil temperature, irrespective of season, but being severely restricted by drought and, perhaps, by competition for photosynthate from above-ground organs (Lesham, 1965; Roberts, 1976; Persson, 1978; Deans, 1979).

Estimation of rate of root death is difficult. Recent direct measurements of the variations in root necromass by both Persson (1978, 1979, 1980) and Kinerson *et al.* (1977) suggest ratios of about 1.75 for increase in root necromass on weight of leaf-litter production for *Pinus sylvestris* and *P. taeda*, the ratio decreasing to 0.75 if measured recruitment to dead branches is included for the latter.

As the nutrient content of recently dead roots is not known, measurements of nutrient release from this source remains unquantified. There are, in addition, further losses, such as those resulting from release in root exudates and from death of mycorrhizal hyphae. Smith (1976) estimated that in mixed hardwood species unsuberized roots can exude about 8 kg K and over 3 kg Ca $ha^{-1} yr^{-1}$; for other nutrient cations the values were less than 1 kg. Fogel and Hunt (1979) have published estimates for organic matter turnover in mycorrhizas on the basis of which Fogel (1980) suggested that N turnover through mycorrhizas is greater than that for the rest of the tree, although the considerable difficulties in measurement must counsel caution until further data becomes available.

Thus, there is little reliable information on the rate of release of nutrients from below-ground organs. It is probably high, although due to its form and position much of that released below ground is likely to be readily reabsorbed by living roots. Turnover of fine roots and their roles in nutrient cycling are discussed further in Chapter 6.

(3) Nutrient uptake

In view of the difficulties of assessing crown leaching and below ground turnover, there are probably no completely accurate measures of nutrient uptake. Nevertheless, for some elements the published estimates must be

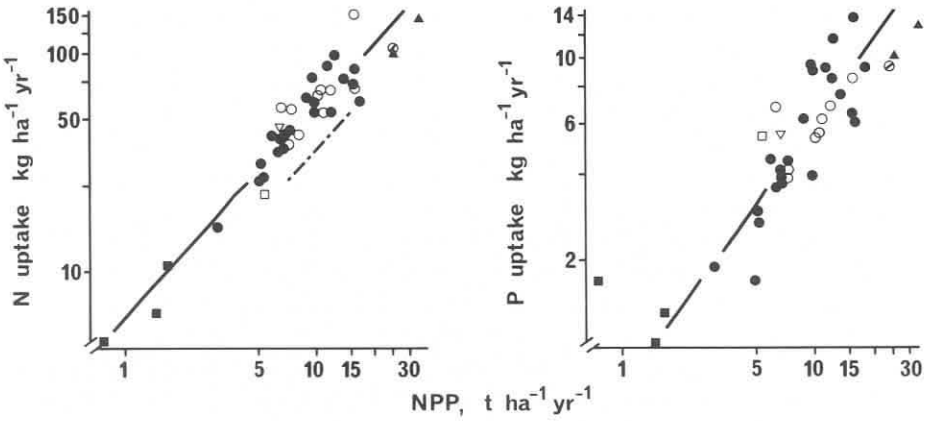

Fig. 5. Uptake of nitrogen and phosphorus into above-ground components as a function of net primary production (NPP) using data reported for coniferous forests from boreal (■), temperate (●) and tropical (▲) regions and for broad-leaved forests from boreal (□), temperate (○, ⊘ *Alnus rubra*) and mediterranean (▽) regions. Uptake is calculated as change in accumulation over time plus release in litterfall. Both regressions are significant at $P<0.001$, r^2 values being 0.90 and 0.74 for N and P, respectively. Broken line on N graph shows the minimum N uptake predicted by the model of Miller *et al.* (1976) as being necessary to sustain growth of *Pinus nigra* var. *maritima* over the illustrated range. Plotted data are taken from Cole and Rapp (1981), Foster and Morrison (1976), Mälkönen (1974), Mälkönen (1977), Miller and Miller (1976), Miller *et al.* (1976), Nihlgård (1972) Ovington and Madgwick (1959a, b), Paavilainen (1980).

fairly close, particularly for those such as N and P for which crown leaching seems to be a minor process. Estimates range widely (Table VI), which is hardly surprising in view of the range of growth rates encountered across the world. As both rate of accumulation and rate of release in litterfall are primarily functions of growth rate, with relatively little differences resulting from necessary specific variations in nutrient concentrations, a common relationship between uptake and net primary production might be expected. The limited data so far available indicates that this is broadly true (Fig. 5). Variations about the regressions in Fig. 5, although fairly large, indicate no assortment by species or region other than through the effects on growth rate. In particular there is no suggestion that coniferous forests require less nutrients than do broad leaved, nor that the one alder stand had exceptional N requirement despite its ability to fix atmospheric dinitrogen. The scatter of the points, although undoubtedly partly reflecting both experimental error and the small specific variation that may exist, is probably largely due to differences in soil nutrient supply. Indeed, it may be relevant that the various stands, none of which were considered by the respective authors to be N deficient, all lie above the line calculated from the model of Miller *et al.*(1976) as being the minimum N uptake necessary to sustain the illustrated range of

Table VI. Estimates of nutrient uptake in closed-canopy, even-aged forests.

Genera and location	Element (kg ha^{-1} yr^{-1})					Reference
	N	P	K	Ca	Mg	
Fagus						
Germany	72	5	46	33	3	Ulrich and Mayer, 1972
S. Sweden						
(3 site types)	50–113	5–8	34–49	63–107	5–12	Nihlgård and Lindgren, 1977
Quercus						
Belgium	92	7	69	201	19	Duvigneaud and Denaeyer-De Smet, 1970
England (2 sites)	44–85	3–6	30–60	40–111		Brown, 1974
Oklahoma						
(mixed species)	101	11	80	300	23	Johnson and Risser, 1974
Missouri						
(mixed species)	54	6	29	82	7	Rochow, 1975
Pinus						
S. Finland						
(3 site types)	19–39	2–4	10–15	11–19		Mälkönen, 1974
N. Ontario	26	2	15	19	3	Foster and Morrison, 1976
Central Sweden	6.5	0.6	3.5	6.9	1.1	Bringmark, 1977
Scotland						
—nitrogen deficient	17	4	14	36	8	Miller *et al.*, 1976
—at maximum growth	69	6	28	34	11	
Tanzania	145	13	78	109	32	Lundgren, 1978

growth rates. If the assumptions and data used in the model are correct, it suggests that most stands are taking up rather more N than is immediately required to maintain growth at the rate dictated by light, temperature or water limitations.

The data in Fig. 5 are all for closed-canopy crops. As has already been seen in Fig. 1, however, within any one stand the pattern of nutrient uptake and cycling is very different prior to and during canopy closure than at later stages. This is because whereas net accumulation in tree tissues accounts for most of the uptake until the trees reach 10 m and canopy is closed (the first

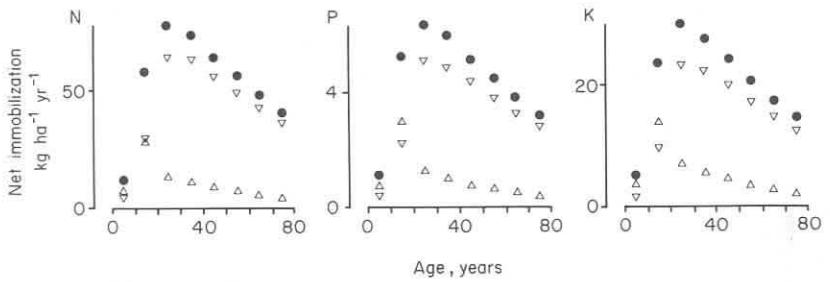

Fig. 6. Calculated mean rates over 10-year periods of net immobilization of nutrients in tree tissues (△), release through litterfall, root death and crown leaching (▽) and total uptake (●). Calculations are based on data for fast growing (maximum mean annual increment 16 m^3 ha^{-1} $year^{-1}$ with tree height ca 10 m at 20 years and 20 m at 40 years) *Pinus nigra* var. *maritima* (Miller *et al.*, 1976; Miller *et al.*, 1979; Miller *et al.*, 1980a, b).

two decades in Fig. 6), thereafter accumulation falls to relatively low values with much of the absorbed nutrients being released to re-enter the cycle.

B. Cycle within the Tree

The sudden drop in rate of net accumulation within the tree after canopy closure (Fig. 6) is not because of reduced rate of tissue formation, indeed maximum annual production of both foliage and wood in this stand does not occur until the next decade contemporary with the maximum rate of leaf-fall. By this time, however, a large proportion of the nutrients required for the formation of new tissues is being translocated from older tissues, particularly from foliage. It has already been pointed out (Table III) that 60–84% of the nutrients in foliage may be recovered before litterfall, and from Table VII it will be seen that retranslocation from all sources can supply between 50 and 60% of the requirements for new growth of these trees. Similarly, Rapp *et al.*

Table VII. Comparison of sinks and sources of major nutrients calculated for *Pinus nigra* var. *maritima*.[a]

	Flux ($kg\,ha^{-1}\,yr^{-1}$)[b]		
Components	N	P	K
Sinks			
In new needles	92	9.4	45
To replace lost structural tissues	20	1.7	4
Net increase in structural tissues	26	3.0	11
To replace leaching losses	0	0.0	6
Total requirements	138	14.1	66
Sources			
Uptake from soil	69	6.0	28
Recovery from needles before death	61	7.2	32
Recovery from other tissues	8	0.9	6
Total of all sources	138	14.1	66

[a] From Miller (1981a).
[b] Values are for a stand of volume $226\,m^3\,ha^{-1}$ and volume increment $19.7\,m^3\,ha^{-1}\,yr^{-1}$ with average needle retention of about 2.4 years.

(1979) estimated that in *Pinus pinea* retranslocation supplied 20.1 kg of the 46.5 kg N ha^{-1} incorporated into new foliage.

Clearly foliage is the most important source of nutrients for the cycle within the tree, but the proportion of the requirement for a nutrient that can be met by retranslocation from dying foliage must vary with age. Thus, during the first two decades of the stand modelled in Fig. 7, there is an imbalance between the number of new needles being formed and the number of old needles being discarded, with consequent limitations on the proportion of the annual nutrient requirement that can be met by retranslocation. Indeed, although the N requirements for new needles at ages 10 and 40 years are very different, the amount of N required over and above that retranslocation from older foliage is identical at the two ages.

The imbalance between production and loss of foliage during the first two decades reduces with decreasing years of foliage retention, being least in deciduous species which necessarily have to renew the entire foliage mass every year. This leads to interesting speculation as to where the retranslocated nutrients are stored pending the resumption of growth, for, not only in deciduous species but also in most evergreen species, the time of maximum leaf-fall is seldom coincident with the time of maximum leaf production. Studies in deciduous fruit trees have shown considerable conversion of protein to amino acids in twigs just prior to bud burst (e.g. David and David,

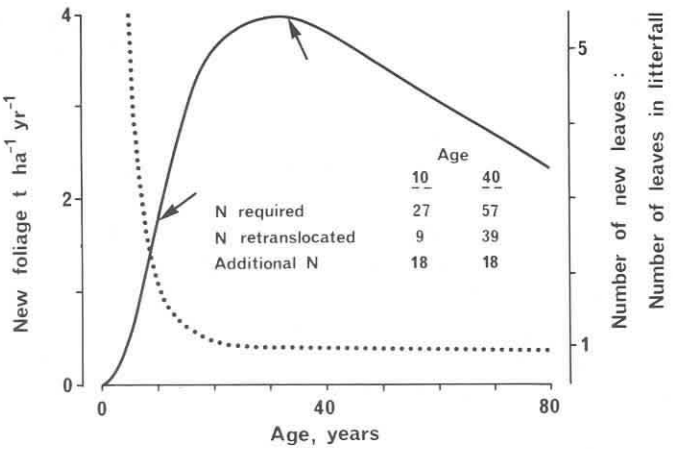

Fig. 7. Pattern of production of new foliage (——) and ratio of number of new leaves produced to number discarded in litterfall (· · · · · · · ·), assuming a 3-year leaf retention period, for *Pinus nigra* var. *maritima* (Miller *et al.*, 1980a and unpublished data). Table gives fluxes of nitrogen, kg ha^{-1} yr^{-1}, calculated as being necessary to maintain the illustrated rates of foliage production at ages 10 and 40 years (arrowed).

1966; Tromp and Ovaa, 1971), suggesting that the twigs are an important storage site, at least of N, over the leafless period. It seems probable that roots also act in this way (van den Driessche and Webber, 1977) (see Chapter 6).

Fagerstrom and Lohm (1977) have emphasized the advantages of thinking in terms of mobile (or potentially mobile) and non-mobile (structurally bound) forms of a nutrient within the tree, the amount of the mobile form of a limiting element being the primary determinant of growth rate. Miller *et al.* (1979) developed on this by suggesting that the sources of mobile nutrients available for retranslocation fall into two categories on the basis of their mobility. The first covers the temporary seasonal storage of nutrients recently either recovered from dying tissues or taken up by the roots. Unless deficiencies arise, these would represent the only sources of mobile nutrients other than contemporary root uptake, tapped by the tree for its new growth. The second source includes those potentially mobile forms that can be used to make up, at least in part, for an inadequate supply from the sources that contribute to the first category. This can be by mobilization of reserves previously accumulated in excess of the requirements for growth, as can happen during heavy fertilizer application. Such mobilization was alone sufficient to explain the enhanced growth rate in *Pinus nigra* var. *maritima* during the years after cessation of fertilizer application (Miller *et al.*, 1976).

Sometimes, however, mobilization from the second category occurs at a sub-optimum level of nutrition and can impair the proper functioning, or even existence, of older tree tissues. Thus, it has been frequently observed that N deficiency reduces the age at which needles senesce (e.g. Miller and Miller, 1976; Turner and Olsen, 1976).

At one level, therefore, the nutrient cycle within the tree can be regarded as enabling storage both of nutrients retranslocated from dying organs, notably foliage, and of nutrients taken up during the dormant period, so allowing efficient conservation of a nutrient and accumulation pending the pronounced demands of new tissues formed during the, sometimes fairly short, growth period. At a second level the internal cycle is, at least conceptually, rather different, enabling storage during plentiful supply for use in possible future lean years. This explains much of the longevity of the response shown by trees to fertilizer application and their ability to show a fairly regular pattern of annual growth despite marked variations in soil nutrient supply. For this reason the concept of "luxury uptake", implying useless accumulation, is not applicable to large perennial plants.

C. Accumulation and Release in Soil Organic Layers

The pattern of accumulation of tree litter on the soil surface throughout the life of a plantation appears to follow a rather sinuous trend (Fig. 8), declining rapidly from clear-felling until the new crop closes canopy, and then increasing to reach a maximum about a half to two-thirds of the way through the rotation. The size of the maximum varies considerably with factors of the site, in particular the latitude (Tsutsumi, 1971), there being generally a smaller accumulated weight beneath tropical forests than beneath temperate or boreal forests. As rate of litterfall is higher in fast growing tropical forests this implies that decomposition in these forests must be very rapid. Indeed, turnover rates of organic matter appear to be frequently of the order one year or less in tropical forests (Cole and Johnson, 1978), as against 5 to 20 years in many temperate and boreal coniferous forests. However, at any one latitude, species differences do occur, and even within species there may be considerable differences in decomposition rates, reflecting soil factors, notably N status and acidity (see Chapter 5).

Accumulated nutrients broadly follow the same trend as organic matter, although the rapidity with which different elements are released varies greatly, generally being fastest for the metallic cations and slowest for N, with P occupying an intermediate position. There is even a suggestion that because of the high C:N ratio in humus, there might be a continuing

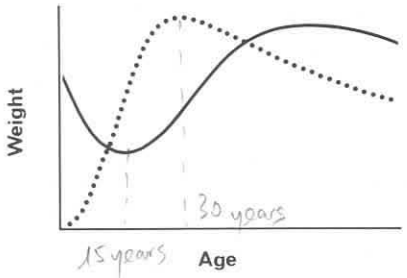

Fig. 8. Hypothetical patterns of rate of litterfall (· · · · · ·) and accumulated weight of soil organic layers (——) in a second rotation plantation (y values not to the same scale) drawn from various sources (e.g. Aber *et al.*, 1978; Lundgren, 1978).

accretion of N long after organic matter accumulation has stabilized (Foster and Morrison, 1976). This immobilized N may be regarded, in the short-term, as N lost from the cycle within the forest and can lead to the gradual development of deficiency conditions on sites already low in this nutrient.

Whether this type of a N deficiency can occur in broad-leaved deciduous forests is not clear. There seem to be no such reports, probably reflecting differences in decomposition patterns between species (Heal, 1979), although it may partly be because broad-leaved species are generally found on soils of higher N capital. Although difficult to substantiate, there does seem good reason to suspect that, in general terms and irrespective of species, the quality of litter, with respect to ease of decomposition, declines with decreasing N status of the site.

III. INPUT AND RETENTION OF NUTRIENTS

A. Inputs

Inputs to a plantation arrive in precipitation, aerosols, dust, gases etc., or, in the case of gaseous dinitrogen, by microbial and symbiotic fixation. The weathering of soil minerals also contributes to the pool of available soil nutrients and, although strictly a transformation within the ecosystem rather than a net addition to it, over the short-term this is best considered as an input.

(1) Input in precipitation and through the filtering effect

Rain, snow and hail bring with them appreciable quantities of most plant nutrients, in addition to which there is capture on plant surfaces of

wind-borne particles and gases, a capture that then adds to the nutrient content of rainwater flowing over the plant (Table IV). The size of these nutrient inputs varies considerably with element and location (Table VIII).

Table VIII. Ranges of reported inputs of nutrients to forests in precipitation and through trapping of aerosols and dust on tree surfaces.[a]

Mechanism	N	P	K	Ca	Mg
Bulk precipitation:					
European reports	1–22	0.02–0.50	0.5–20.0	1.0–20.0	0.5–7.0
North American reports	2–9	0.07–2.30	0.2–3.0	0.4–10.0	0.1–13.0
Trapped aerosols and dust	0–4	0–0.2	4–6	4–6	0.5–2.0

[a]Data from Mayer and Ulrich (1974), Horntvedt (1975), Miller *et al.* (1980b); Cole and Rapp (1981).

In particular, the capture of wind-borne elements, termed the "filtering effect" by Mayer and Ulrich (1974), may lead to relatively large inputs of S and trace elements such as Pb, in areas of high atmospheric pollution (Ulrich *et al.*, 1976; Lindberg *et al.*, 1979).

Much of the N and a small proportion of the P in precipitation is in organic form, but the soluble forms of other elements appear to be entirely inorganic. The origin of most of these ions seems to be the oceans (O'Carrol and McCarthy, 1973; Hingston and Gailitis, 1976), with limited contributions from terrestrial dust, particularly of K and Ca. In addition, elevated levels of sulphates, nitrates and some trace elements, such as Pb and Hg, can occur in rain from air masses that have previously passed over industrial areas, even when these are many hundreds of kilometres upwind. This long-range transport of air pollutants and "acid rain" is now causing concern in Europe and North America.

The existence of a "filtering effect" in forests has been deduced for some time (e.g. Eriksson, 1959), but only recently have measurements of its amount and composition become available (Table VIII). Studies in Europe and North America show that industrial pollution, particularly with S compounds, can contribute greatly to this input, but there are in addition many salts that are largely sea-derived. This process has been termed "dry deposition", in contrast to the wet deposition in precipitation, and this distinction is still useful in some studies. More recently, however, it has been realized that the filtering effect is more than the capture of gases and dry particulate matter, for it includes the capture of water-borne material, as mist, fog and fine raindrops, that is not adequately collected by a standard rain gauge.

(2) Nitrogen fixation

This is dealt with in detail in Chapter 13 so discussion here is limited to a brief examination of its importance in nutrient cycling. On a world-wide scale biological N fixation averages $10\,kg\,ha^{-1}\,yr^{-1}$ (Kormanik, 1979). Estimates for forests, excluding those of nodulated species such as *Alnus* which are known to achieve peak annual rates of up to 300 kg N ha^{-1} (Tarrant *et al.*, 1969), include values of 0.4–3.5 kg for Swedish forests (Granhall and Lindberg, 1978) and 5–35 kg estimated by Knowles (1965) from extrapolation of laboratory results. Because no recent budget study has indicated an annual accretion of N in the ecosystem significantly greater than the input in precipitation, it would seem that non-symbiotic fixation in forests is at the lower end of this scale and is unlikely to make more than a small contribution. However, the deliberate inclusion of N fixing species in the tree canopy or under-storey of a plantation (e.g. Gadgil, 1971) can be very beneficial and presents an exciting challenge to future silviculturalists.

(3) Mineral weathering

Maintenance of the pool of available nutrients in soil is dependent on ion exchange and on the weathering of minerals (see Chapter 4). Tree growth processes, by removing cations from the available pool and through the efflux of H^+ from roots, accelerate the weathering reactions required to replenish this pool. Measurements of soil nutrient supplies are fraught with difficulties of sampling and interpretation, but some studies have shown a reduction of exchangeable nutrients, and an increase in acidity, beneath trees early in the rotation (e.g. Williams *et al.*, 1978). The rate of recharge is then less easily quantified, but studies by Lundgren (1978), beneath an age series of plantations on latosols in Tanzania, showed that levels of exchangeable Ca, Mg and K in the top 10 cm of soil declined markedly during the period of intense uptake associated with canopy closure, but that thereafter replenishment of the available pools of Ca and Mg was very rapid. However, for K, for which the total reserves were low, rate of replenishment was slow. Clearly any attempt to measure the effects of trees, and timber harvesting, on soils should take cognizance of these dynamic aspects.

B. Retention within the Ecosystem

Nutrient inputs and the nutrients released by the trees through crown leaching, or through decomposition of litter, are only of value if they are

retained within the cycle in a form suitable for root uptake. The organic layers and surface mineral horizons of forest soils let remarkably small amounts of nutrients leach through to deeper horizons. This is in part due to chemical adsorption, but the particular feature of forests that maintains "tight" nutrient cycles is the efficiency with which the vast network of mycorrhizal hyphae ensure that few ions remain in the soil solution long enough to be leached out. An extreme example comes from the forests of Venezuela where less than 0.1% of radioactive tracers of several nutrient elements applied to the surface leached through the root mat (Stark and Jordan, 1978).

It follows that retention of nutrients in the ecosystem, particularly a limiting nutrient, will be most pronounced during the period of maximum tree uptake early in the rotation (cf. Fig. 6), with minimum retention during the brief period between clearfelling and revegetation with weed species. Experimental verification of the accelerated loss of nutrients from areas kept bare of vegetation has come from the now well-known study at Hubbard Brook (Likens *et al.*, 1977) (see Chapter 14). Vitousek and Reiners (1975) have then pointed out that as nutrient demands fall with age there comes the possibility of a gradual increase in losses as progressively tree demands fall below the rate of soil nutrient supply.

This efficient nutrient retention is a pronounced and important feature of forests, and one that distinguishes them from most other forms of managed vegetation (e.g. Dillon and Kirchner, 1975). Indeed, Miller *et al.* (1976) found that a N-deficient closed-canopy plantation of *P. nigra* var. *maritima*, retained all of a total of 252 kg fertilizer N ha^{-1} applied over 3 years, more than half within the tree biomass, although at higher rates, losses increased linearly. Fertilizer P is similarly retained, both by biological uptake and, except on peaty soils (Malcolm *et al.*, 1977), by chemical adsorption in the soil, whereas K, which is very mobile, is retained by being incorporated into the rapid cycle of this element (Stone and Kszystniak, 1977; Miller *et al.*, 1979).

Leaching losses of essential and scarce nutrients from forests, therefore, are likely to be slight except either very early or very late in the rotation. Harvesting losses have long been suggested as a possible cause for concern (Rennie, 1955), and the recent prospect of whole-tree harvesting has stimulated renewed interest (e.g. Weetman and Webber, 1972; Malkonen, 1976). However, Miller *et al.*, (1980a, b) modelled the effect of different harvesting policies and growth rates on nutrient removal in pine under Scottish conditions and concluded that only very intensive harvesting of fast-grown trees is likely to remove much more than the expected atmospheric input of most nutrients, even in areas of fairly low inputs, the exception being P for which atmospheric inputs never matched harvesting removals.

IV. FULL CYCLES AND THEIR SILVICULTURAL IMPLICATIONS

In summary it can be stated that the rates of uptake, accumulation and release in litterfall of a nutrient are largely functions of growth rate. Species differences, although real, are minor after allowance is made for growth rate, but soil supply can have considerable influence, there being strong evidence that established forests will take up nutrients in excess of immediate requirements. This excess uptake is reflected both in the amount released by the trees and in the amount that remains to accumulate in their tissues, with the trees being able to draw on the accumulated reserves to maintain growth during periods of restricted supply. Whether or not crown leaching also increases with growth rate remains unknown, although there are indications of possible species differences.

As the growth rate of a stand shows a progressive variation with age, rates of nutrient cycling may be very different at different stages in the rotation. However, the gradual increase in the amount of each nutrient being cycled within the forest means that variations in rate of uptake throughout the rotation do not simply reflect variations in growth. The trees in the older of the two stages detailed in Table IX can meet much of their nutrient requirements through retranslocation, so the rates of uptake from the soil are not very different between the two, despite the much larger total requirements of the older trees. Furthermore, the older trees release a greater proportion of their annual uptake to recycle through the soil. Because of the development of these rapid cycles, both within the trees and within the ecosystem, and because of enhanced trapping of atmospheric elements through the filtering effect, the rate of reduction in the total amounts of N, P and K in the soil beneath the larger trees is only 8–45% of that when the trees were young. Indeed, for Mg, the rate of transfer from soil to tree has become less than the atmospheric input.

Consideration of these changes in the pattern of nutrient cycling with age (Miller, 1981b) suggests three nutritional stages in the life of a plantation. During the years prior to canopy closure (Stage I), tree growth is very dependent on the current uptake of soil nutrients and responses to applications of fertilizers are common. Once canopy has closed, the reduction in rate of accumulation of nutrients associated with attaining maximum foliage biomass, the development of rapid nutrient cycles and the efficient capture and retention of atmospheric nutrients means that, at this stage (Stage II), the demands made on the soil nutrient capital may have fallen to the extent that soil supplies are seldom inadequate and fertilizer responses are unlikely. However, should the nutrient capital in the cycle ever be reduced, for example by destruction of a significant proportion of the foliage biomass,

Table IX. Comparison of rates of transfer and accumulation of nutrients modelled for a 10-year-old, 2 m-tall stand and a 40-year-old, 11 m-tall stand of *Pinus nigra* var. *maritima*.[a]

Transfer		Nutrients ($kg\ ha^{-1}\ yr^{-1}$)							
		10-year-old stand				40-year-old stand			
		N	P	K	Mg	N	P	K	Mg
Net immobilization in new tree tissues	(A)	56	5.7	25	4.7	87	10.2	49	6.8
Release from trees	(B)	10	1.0	4	2.2	51	3.9	17	7.2
		—	—	—	—	—	—	—	—
	(A + B)	66	6.7	29	6.9	138	14.1	66	14.0
Tree uptake	(C)	55	5.5	22	6.3	69	6.0	28	10.9
Retranslocation within tree	(D)	11	1.2	7	0.6	69	8.1	38	3.1
		—	—	—	—	—	—	—	—
	(C + D)	66	6.7	29	6.9	138	14.1	66	14.0
Net immobilization in humus	(E)	3	0.3	(0.2)	0.4	12	1.5	1	1.6
Atmospheric input	(F)	5	0.1	6	3.5	5	0.1	10	4.7
Net change in tree stand	(C − B)	+45	+4.5	+18	+4.1	+18	+2.1	+11	+3.7
Net change in soil capital	(B + F − C)	−40	−4.4	−12	−0.6	−13	−2.0	−1	+1.0

[a] Summarized from Miller *et al.* (in press).

then fertilizers may accelerate recovery. This would explain the frequent observation that closed-canopy stands are most likely to respond to fertilizers when combined with a thinning, an operation that temporarily removes a large proportion of nutrients, those bound in the dying foliage on the slash, from the cycle. Similarly, fertilizers can be used to accelerate recovery after attack by defoliating insects. There remains a further stage (Stage III), most usually reported for coniferous plantations in high latitudes, represented by late rotation N deficiency resulting from temporary removal from the cycle, through immobilization in humus, of an unacceptable amount of N. On many sites there is sufficient N to prevent this stage ever developing, whereas on others, including vast areas of the Douglas fir region in Western North America, forests enter Stage III fairly soon after canopy closure. They then remain incipiently N-deficient for the rest of the rotation, or until the declining N requirement with age falls to match the rate of soil supply. To date, the only management option, other than accepting a slow rate of growth, is to apply N fertilizer, but the hope remains that it may become possible, perhaps through thinning or other silvicultural techniques, to manipulate the rate of release of N from humus (see Chapter 5).

Consideration of the pattern of nutrient cycling in plantations, therefore, leads to the realization that nutrient deficiencies are essentially problems of youth and old age—a realization that goes some way to explaining otherwise puzzling anomalies in fertilizer response. In this and other ways the study of nutrient cycling is enabling the establishment of a rational basis to forest nutrition. A basis that will provide the forest manager with a conceptual framework to assist him in extrapolating to his particular circumstances the limited and restricted results available from empirical experimentation.

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